EARLY DEVONIAN (EMSIAN) VERTEBRATE MICROREMAINS FROM THE BUCHAN GROUP, VICTORIA, AUSTRALIA

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The vertebrate microfauna from the Early Devonian Buchan Group in northeastern Victoria is dominated by remains of acanthodians and placoderms, with osteichthyans less common, and chondrichthyans and thelodonts rare. Acanthodian remains include scales of *Nostolepoides platymarginata, "Nostolepis" gnangxiensis, Gomphonchus? bogongensis*, scales similar to those of *Cheiracanthoides comptus* and *C. wangi*, and possible *Rhadinacanthus* scales. Scales of arthrodires *Goodradigbeeon* and *Buchanosteus* are the most abundant placoderm remains; placoderm plate fragments are attributed to *Buchanosteus* and *Murrindalaspis*. Osteichthyan remains include a scale of the actinopterygian *Ligulalepis toombsi*, and onychodont scales and teeth. Taxa previously undescribed from Buchan are acanthodians *"Nostolepis" gnangxiensis, Cheiracanthoides* sp. cf. *C. wangi* and *Rhadinacanthus*, chondrichthyan *Ohiolepis* sp., and osteichthyan *Ligulalepis toombsi*.

Key words: Early Devonian, Emsian, vertebrate microfossil, acanthodian, placoderm, chondrichthyan, osteichthyan

DEVONIAN fossil fish remains have been known from the Buchan area of northeastern Victoria for well over a century. McCoy (1876) described as '*Asterolepis ornata* var. *australis*' a plaeoderm bone that has subsequently been shown to be portion of the skull of a large arthrodire (Young 1979). From the same area, an almost complete arthrodire skull was initially described by Chapman (1916), subsequently prepared in hydroehlorie aeid by Hills (1936) who referred it to the European genus *Coccosteus*, and eventually assigned to the new genus *Buchanosteus* by Stensiö (1945). Hills (1936) also deseribed a mandible of the lungfish *Dipnorhynchus* from the same area.

The only reeent deseription of maerovertebrate material from Buchan is by Long (1984a), who assigned various disarticulated plates from the McLarty Member of the Murrindal Limestone to *Buchanosteus confertituberculatus*, and deseribed two new acanthothoraeids, *Murriudalaspis wallacei* and *M. bairdi*. He identified several forms first deseribed from the coeval Taemas/Wee Jasper fauna in southern New South Wales: brachythoraeids *Arenipiscis westolli, Errolosteus* sp. ef. *E. goodradigbeensis*, and *Taemasosteus maclartiensis*, and petaliehthyid *Wijdeaspis warrooensis*. Long (1984b) illustrated another *Buchanosteus* speeimen, whieh ineluded seales deseribed by Burrow & Turner (1998, 1999). The only other vertebrate mieroremains known from the Buehan region are seales of the dipnoan *Dipnorhynchus* illustrated by Thomson & Campbell (1971, figs 86-88).

The Early Devonian Buehan Group at Buehan, Victoria (Emsian: *dehiscens - serotinus* zones) comprises three formations (Fig. 1). The Buehan Caves Limestone, predominantly ealearenites and ealeisiltites with dolomites and dolomitie limestones (*dehiscens* Zone) is overlain by the nodular and impure limestones and shales of the Taravale Formation (*dehiscens - serotinus* zones) and the well-bedded and massive limestones with subordinate mudstones of the Murrindal Limestone (*perbonus* Zone). Detailed geology and eonodont biostratigraphy were diseussed by Mawson (1987) and Mawson et al. (1988, 1992).

Other studies have demonstrated the generally fossiliferous nature of these horizons, describing an invertebrate fauna of abundant stromatoporoids and corals assoeiated with braehiopods, bivalves and ostraeods in the Buehan Caves Limestone (Webby et al. 1993; Talent 1995), and more diverse faunas of braehiopods, corals, and trilobites, the oldest known ammonoids, daeryoeonarids, ostraeods, agglutinated foraminiferans, seolecodonts and chitinozoans in the overlying Taravale Formation (Teichert & Talent 1958; Mawson 1987; Winchester-Seeto 1996).

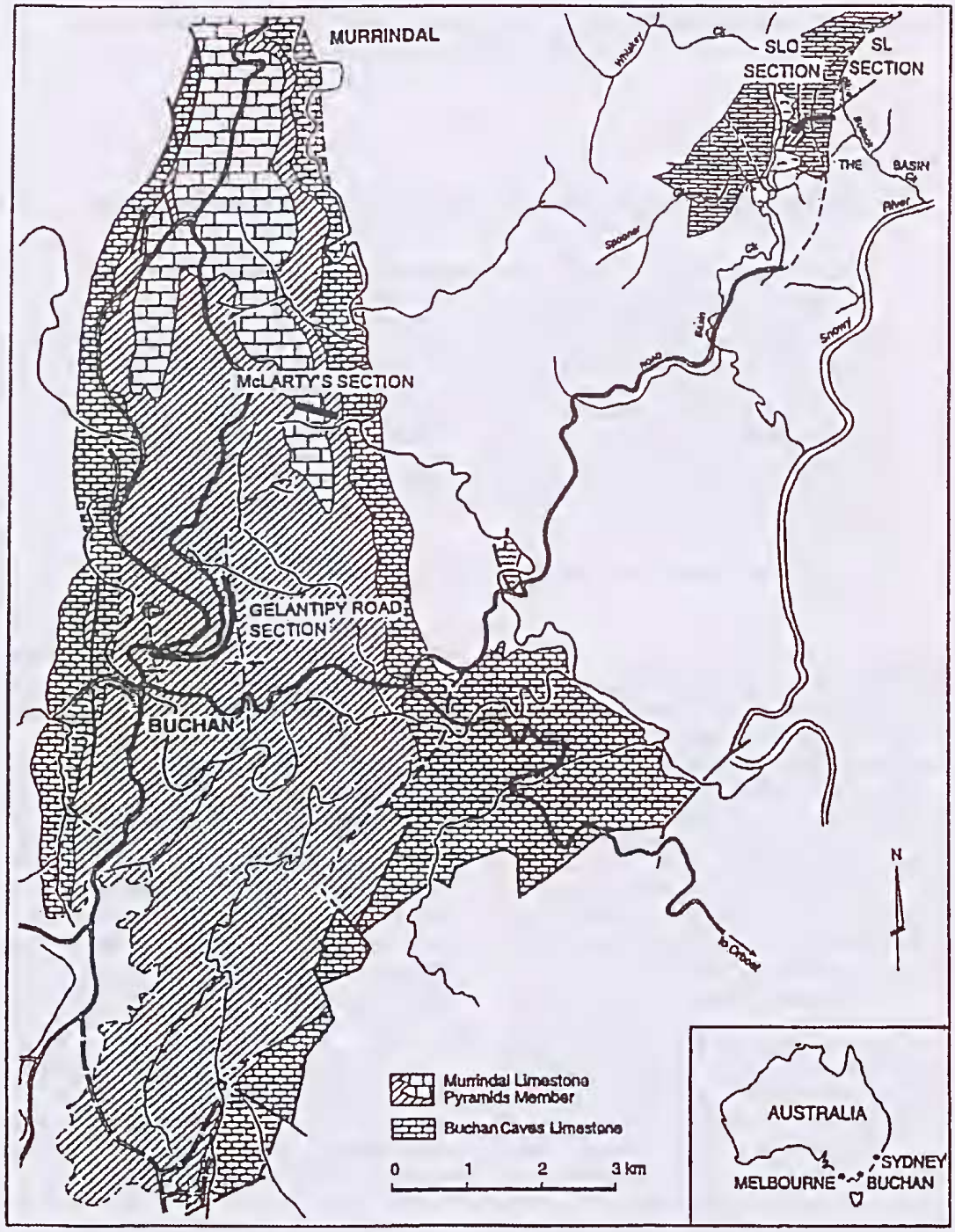


Fig. 1. Geology of Buchan Group around Buchan and The Basin, eastern Victoria (modified from Mawson et al. 1992 and Winchester-Seeto 1996).

Bed-by-bed sampling of long stratigraphic sections through the Buchan Group (Mawson 1987; Mawson et al. 1988, 1992) has resulted in acetic acid-insoluble residues containing both conodonts and microvertebrates. Identifiable microvertebrate remains occurred in three sections (Slocombe's - SL/SLO, 42 samples; McLarty's – Mc, 120 samples; and Gelantipy Road - G.Rd, 80 samples), spanning the *dehiscens, perbonus* and *inversus* zones. The turiniid thelodont scales from these sections, referred to *Turinia* sp. cf. *T. australiensis*, have been published elsewhere (Basden 1999a). This paper describes and figures the remaining microvertebrate taxa. The present study has increased the known geographic ranges of acanthodians *"Nostolepis" guangxiensis, Cheiracanthoides* sp. cf. *C. wangi* and *Rhadinacanthus*, chondrichthyan *Ohiolepis* sp., and osteichthyan *Ligulalepis toombsi*, all of which are reported for the first time from Buchan.

In the systematic descriptions below, the following abbreviations are used for measured stratigraphic sections: **SL/SLO:** Slocombe's section at The Basin, near Buchan, Buchan Caves Limestone and Taravale Formation, *?pireneae-dehiscens-perbonus* zones; **Mc:** McLarty's section near Buchan, Pyramids Member of Taravale Formation and Murrindal Limestone, *?dehiscens-perbonus* zones; **GRd:** Gelantipy Road section at Buchan, Taravale Formation, *perbonus-inversus* zones (See Fig. 1).

Samples are identified by the section prefix followed by the true height in metres above base of section (indicated by "m"). This is to distinguish between the true height above base of section, used in this study, and the sample number given by Mawson (1987), Mawson & Talent (1994), and Mawson et al. (1988, 1992) at the time of collection, which indicated measurement along the ground. Figured specimens are held in the palaeontology collections of the Australian Museum, Sydney, and bear the prefix AMF.

SYSTEMATIC PALAEONTOLOGY

Superclass **Gnathostomata** Gegenbauer 1874
Class **Placodermi** M'Coy 1848
Order **Acanthothoraci** Stensiö 1944
Family **Weejasperaspididae** White 1978
Genus **Murrindalaspis** Long 1984

Diagnosis (Long 1984a; Long & Young 1988). Dermal ornament of short crenulate ridges, approximately one-third as long as broad, and zones of stout polygonal or stellate tubercles. Body scales rhombic with anterior overlap flanges; exposed area with similar ornament to dermal bones.

Murrindalaspis sp.
Fig. 2A

Material. AMF101198 from Mc41.5-42.7m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), plus seven other scales and fragments from Mc3.4-3.6m, 8.5m, 18.6-21.3m, 27.7-30.5m, 41.5-42.7m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), and Mc156.1m, 180.1m (Murrindal Limestone, *perbonus* Zone).

Remarks. Long (1984a) erected the genus from medial dorsal plates recovered from the Murrindal Limestone (*perbonus* Zone) near Buchan, Victoria. The only other described specimens from southeastern Australia are a sclerotic capsule and associated plates and body scales from the *Receptaculites* Limestone near Taemas (Long & Young 1988:74, figs 9, 10) and three body scales from the same sample (Burrow & Turner 1998:687, figs 10A-E), and a preliminary report of similar scales or plate fragments from the Lochkovian-Pragian Garra Limestone in central NSW, the Murrindal Limestone, and the upper Cavan Formation (*dehiscens* Zone) at Taemas (Basden et al. 2000, fig. 7.1).

Description and Discussion. The scale crowns and plate fragments are ornamented with elongate or stellate tubercles with radiating ridges that appear nodular under high magnification. Long & Young (1988) described the elongate tubercles on the plates as being 3 to 7 times as long as wide, and Burrow & Turner (1998) specified 4-20 nodose radiating ridges on each tubercle.

The scales are generally rhombic or subcircular, with diameter 1-2mm, and a thin margin that can be either faintly radially grooved or granular-textured. Neighbouring scales overlap this thin basal margin (Long & Young 1988), which can extend all around the scale, or be confined to the anterior and lateral margins. The base varies from deeply concave with openings into the tubercles, to gently concave with no canal openings, to flat. Tubercle length varies, with central elongate tubercles, aligned antero-posteriorly, surrounded by 3-12 smaller or more circular tubercles. Commonly, anteriormost tubercles tend to be lower and rounded, and those at the posterior flatter and blade-like.

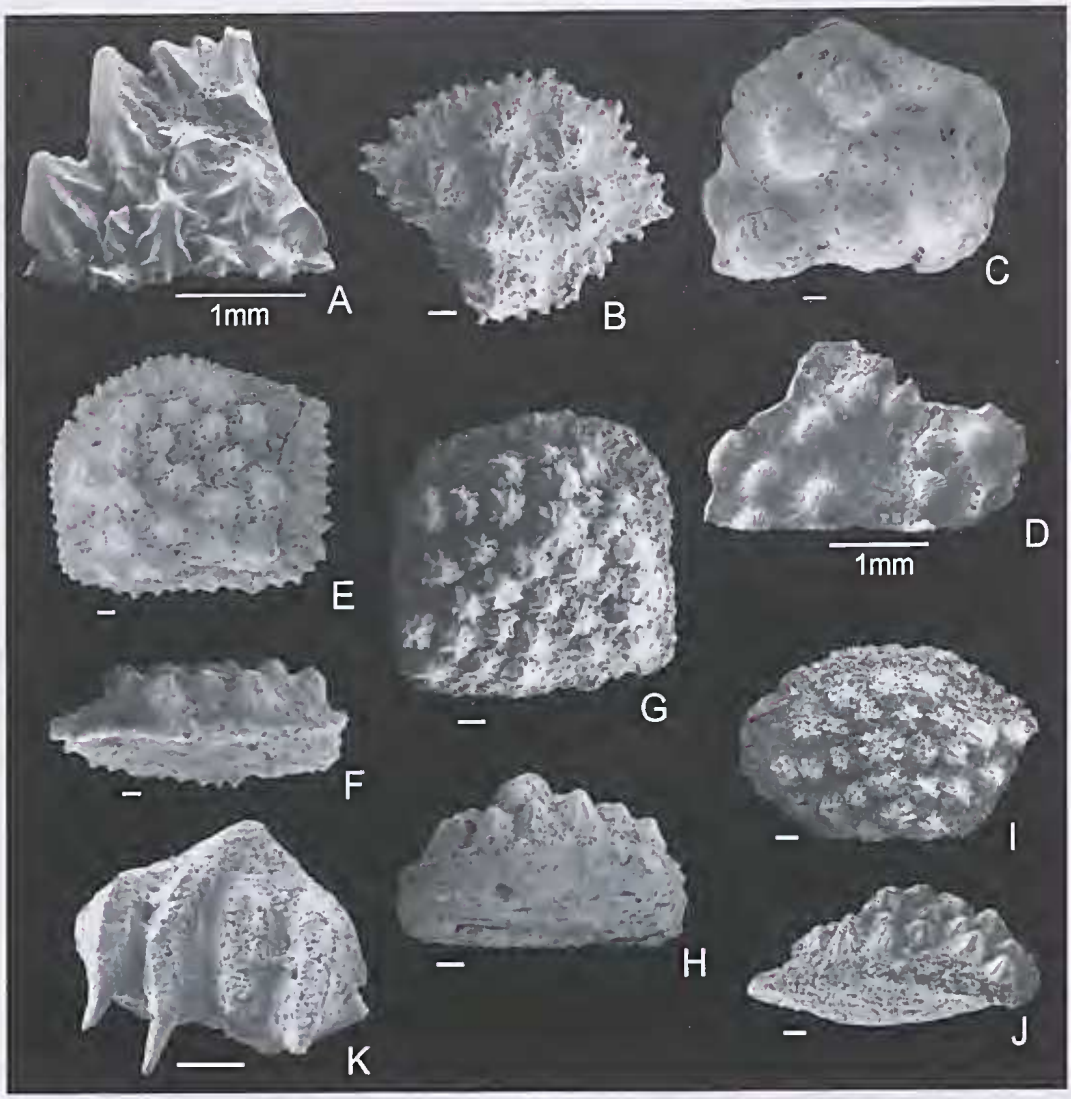


Fig. 2. Placoderm and chondrichthyan microremains from the Buchan Group. Scale bar = 100µm unless indicated otherwise. A, *Murrindalaspis* sp. Fragment AMF101198 from Mc41.5-42.7m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. B-D, *Buchanosteus* sp. B, Scale AMF101199 from SLO51-68m, Taravale Formation, *perbonus* Zone, crown view. C, Fragment AMF112353 from Mc41.5-42.7m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. D, Fragment AMF101197 from GRd340.5m, Taravale Formation, *inversus* Zone. E-J, *Goodradigbeeon australianum* E, F, Scale AMF112355 from SLO213m, Taravale Formation, *perbonus* Zone. E, crown view, F, lateral view. G, H, Scale AMF101196 from SL46.5m, Buchan Caves Limestone, *dehiscens* Zone. G, crown view, H, laterobasal view. I, J, Scale AMF112356 from SL46.5m, Buchan Caves Limestone, *dehiscens* Zone. I, lateral view, J, crown view. K, *Ohiolepis* sp. Scale AMF101180 from Mc91.4-93m, Murrindal Limestone, *perbonus* Zone, crown view. Some of these specimens were illustrated by Basden et al. (2000): A, fig. 10.3; B, fig. 10.4; D, fig. 10.2; G, fig. 10.1; K, fig 8.9.

Burrow & Turner (1988:687, figs 10B, C) described and illustrated histological features of *Murrindalaspis wallacei* scales.

Order **Arthrodira** Woodward 1891
Suborder **Brachythoraci** Gross 1932
Family **Buchanosteidae** White 1952

Genus **Buchanosteus** Stensiö 1945
Buchanosteus sp.
Fig. 2B-D

Material. AMF101199 from SLO51-68m (Taravale Formation, *perbonus* Zone), AMF112353 from Mc41.5-42.7m (Pyramids Member of Taravale

Formation, *dehiscens* or *perbonus* zone), AMF101197 from G.Rd340.5m (Taravale Formation, *inversus* Zone), plus 98 other scales and fragments from SL 39m, 40.8m, 42m (Buchan Caves Limestone, *pireneae or dehiscens* Zone), SL 46.5m, 49.7m, 54m, 56.2m, 58.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO 17m, 34m, 51m (Taravale Formation, *dehiscens* Zone), SLO 64m, 51-68m, 213m and G.Rd 51.2m, 51.7m, 52.5m (Taravale Formation, *perbonus* Zone), Mc 4.9-6.2m, 6.5-7.6m, 11-12.2m, 12.5-137m, 14-15.2m, 15.5-18.3m, 17.7m, 18.6-21.3m, 21.6-24.4m, 27.7-30.5m, 35.4-36.6m, 38.4-39.9m, 41.5-42.7m (Pyramids Member of Taravale Formation, *dehiscens or perbonus* Zone), Mc 88.7m, 91.4-93m, 144.8-146.3m, 156.1m, 161.5m, 189.9m, 192.5m (Murrindal Limestone, *perbonus* Zone), and G.Rd 340.5m, 343.5m (Taravale Formation, *inversus* Zone).

Remarks. The genus has undergone a series of name changes since the holotype was collected near Buchan early last century (Young 1979; Long 1984a, 1995): Chapman (1916) described the specimen as a new species of *Phlyctaenaspis*, it was reassigned by Hills (1936) to *Coccosteus*, and then by Stensiö (1945) to the new genus *Buchanosteus*. White (1952) gave Stensiö's genus a formal diagnosis, and described a similar skull fragment from Burrinjuck as *B. murrumbidgeensis*. White & Toombs (1972) subsequently referred the Burrinjuck material to a new genus, *Parabuchanosteus*. Following study of new specimens from Burrinjuck and re-examination of Chapman's type material, Young (1979) concluded that only one species, *Buchanosteus confertituberculatus* (Chapman), was represented.

In early reports, placoderm scales from Burrinjuck (Ørvig 1969; Giffin 1980) were identified as *Ohioaspis* because of their resemblance to the North American type material of *Ohioaspis tumulosus* Wells 1944. Turner & Murphy (1988) distinguished between *Ohioaspis* scales and similar scales from Nevada, Australia (Burrinjuck) and south China that they called 'buchanosteid-type', because of differences in tubercle morphology.

Burrow & Turner (1998:678-687, figs 2, 3, 4A, B, 5A-J, 6, 9C-G)) assigned scales from the McLarty member of the Murrindal Limestone, collected with dermal plates of *B. confertituberculatus* near Buchan (Long 1991), to the same species as the plates. However, Young et al. (2001) have recently reinterpreted the specimen assigned by Long to *Buchanosteus* as a primitive coccosteid rather than a buchanosteid. Burrow & Turner (1998) recognised slight morphological and histological differences from the Buchan material in two types of similar scales from Burrinjuck, which were described as Buchanosteidae indet., with tubercles on the crown either rounded and discrete or stellate and tightly-packed. Scales with stellate tubercles, from Longmenshan section, Sichuan Province, China (*dehiscens/perbonus* zones), with similar histology to buchanosteid scales from Burrinjuck, have been described as Buchanosteidae? indet.; it is likely that several primitive placoderm groups possessed scales with stellate tubercles (Burrow et al. 2000). Plate fragments and both types of scales described below resemble microremains of *Buchanosteus confertituberculatus* held in the Australian National University Collections (e.g. sample CPC16965 from an unknown locality near Taemas).

Description. Thin, subcircular or subelliptical scales, from 0.7mm diameter to 1.8mm long. Three to 20 tubercles per scale are either discrete and rounded or closely-packed and stellate. Radiating ridges sometimes extend to the tip of the tubercle (Fig. 2B). In some scales the tubercles extend to the margin, although most scales have a thin margin with radiating mucus grooves, producing a denticulate outline (Fig. 2B). The base is gently convex, flat, or gently concave, often with a few small canal openings scattered irregularly over the surface.

Plate fragments (Fig. 2C, D) are ornamented with discrete, rounded, often widely-spaced tubercles, with ridges that can radiate from a rounded top or be subparallel (e.g. some tubercles on AMF101197, Fig. 2B). The bone between the tubercles bears canal openings, especially around the base of the tubercles.

Burrow & Turner (1998, figs 3, 4A, B, 6F, G) illustrated histological features of buchanosteid indet and *Buchanosteus confertituberculatus* scales.

Genus **Goodradigbeeon** White 1978
Goodradigbeeon australianum White 1978
Fig. 2E-J

Goodradigbeeon australianum White 1978: 175, pl. 6d-f.
Goodradigbeeon australianum – Burrow & Turner 1998: 678-80, figs 7, 8A-D.
Goodradigbeeon sp. – Basden et al. 2000: 215, 217, figs 10.1, 11.4.

Material. AMF101196 and AMF112356 from SL46.5m (Buchan Caves Limestone, *dehiscens* Zone),

AMF112355 from SLO213m (Taravale Formation, *perbonus* Zone) and 30 other scales from SL39m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL 46.5m, 48.7m, 56.2m, 58.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO8.5m (Taravale Formation, *dehiscens* Zone), SLO213m and GRd51.2m (Taravale Formation, *perbonus* Zone).

Diagnosis. Description of ornament by White (1978): Ornamentation ... is tubercular, the tubercles being of the usual lemon-squeezer type with a relatively small enamel cap. When fresh the vertical ridges are seen to be pustular, the pustules at the apex forming a rosette around the cap, and the ridges of the basal intertubercular network are noticeably sharp ... There is no very marked variation in size or shape of the tubercles ...The distribution of the tubercles is close and even ... The scales are covered with minute editions of the tubercles of the general ornament, but there is usually a smooth margin around the surface. Revised description (Burrow & Turner 1998): Scales have between seven and 21 crown tubercles (average 12); the tubercles are from 0.01 to 0.02 mm wide, and bear from seven to ten radial ridges, which often branch at or near the base. The tubercles are separate, with no over-growth evident. Unlike other scales from placoderms, these have small, centrally-positioned tubercles surrounded by larger tubercles. Only rare scales have (weakly developed) mucus grooves peripherally; width of the tubercle-free crown margin varies from negligible, to about one-third of the scale width.

Remarks. White (1978) erected the taxon based on macro and microremains collected at localities near Taemas and Wee Jasper in southern New South Wales. Burrow & Turner's (1998) examination of scales from the residue of the holotype held in the collection of the Natural History Museum, London, resulted in an expanded description of the scales, and explanation of the histological differences between scales of this genus and those of *Buchanosteus*.

Description. Biconvex scales are subcircular, diamond-shaped or polygonal shaped, with the crown ornamented with 19-34 closely-spaced stellate tubercles. Central tubercles are often smaller. Between seven and ten radiating ridges on tubercles can branch near the base. A tubercle-free zone on the crown margin varies in width from negligible to approximately one-eighth the width of the scale (Fig. 2G). The base has up to three pore openings (Fig. 2H).

Burrow & Turner (1998, figs 4C, 8E) illustrated the histology of *Goodradigbeeon australianum* scales.

Class **Chondrichthyes** Huxley 1880
Subclass **Elasmobranchii** Bonaparte 1838
Order incertae sedis
Ohiolepis Wells 1944

Diagnosis (Wells 1944). Small to relatively large shagreen denticles, rounded rhombic, quadrangular, or irregularly elongate or transversely oval in outline, consisting of a broad crown ornamented by numerous spinelike tubercles with enamelled anteriorly indented, anteriorly sloping faces and acute, posteriorly inclined tips, resting directly on an often internally convex, lamellar base....anterior sides or edges of denticles devoid of tubercles over a narrow strip where overlapped by preceding denticle.

Ohiolepis sp.
Fig. 2K

Material. AMF101180 from Mc91.4-93m (Murrindal Limestone, *perbonus* Zone), plus three other scales from Mc18.6-21.3m, 35.4-36.6m (Pyramids Member of Taravale Formation, *dehiscens or perbonus* Zone), and Mc 91.4-93m (Murrindal Limestone, *perbonus* Zone).

Remarks. The genus, established by Wells (1944) from material from USA, has been reported from Australia (Schultze 1968; Giffin 1980; Turner 1982, 1993; Pickett et al. 1985; Young 1993; De Pomeroy 1994; Burrow 1997), China (Wang 1984; Zhu 2000; Zhu et al. 2000) and Germany (Ørvig 1969; Friman 1983; Vieth-Schreiner 1983). De Pomeroy (1994) discussed the differences between some of these reported occurrences, in particular the morphology and spacing of the spines on the crown, and the shape and structure of the base.

Description. Diamond-shaped scales are 0.5-1.2mm long and 0.5-0.9mm wide. The crown is fairly flat and bears 4-22 closely-packed, conical spines with rounded or pointed tips, that can either cover the crown or leave a smooth, unornamented anterior or anterolateral margin. The anterior face of the spines can be flattened or bear a longitudinal groove that is more developed on the spines with a pointed tip. The groove can extend for about half the length of the spine or almost to the

tip, with spines on the same scale showing variety of groove length. The grooved, pointed spines tend to be more steeply inclined than the smoother, round-tipped spines.

The diamond-shaped base is generally very slightly convex and centrally vaulted. On some specimens, the lateral corners of the base curve down slightly, while on others the base is gently concave with a thin marginal rim. The neck, when present, is shallow and not indented.

Class **Acanthodii** Owen 1846
Order **Climatiiformes** Berg 1940
Family **Climatiidae** Berg 1940
Genus **Nostolepis** Pander 1856
"Nostolepis" guangxiensis Wang 1992
Fig. 3A-D

Gomphonchus guangxiensis (Wang) – Turner et al. 1995: 383.
Gomphonchus? Guangxiensis (Wang 1992) – Burrow 1997: 64-66, pl. 1 figs 4-8, pl. 4 figs 1-6.
"Nostolepis" guangxiensis Wang 1992 – Burrow et al. 2000: 398-399, pl. 5.4-5.8.
?acanthodian E – Basden et al. 2000: fig. 9.13.
?acanthodian H – Basden et al. 2000: fig. 12.3.
"Nostolepis" guangxiensis Wang 1992 – Burrow 2002: 91-95, figs 4E-J, 5J-M, 12A, C, D.

Material. AMF101193 from Me41.5m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), AMF101190 from Me148.1m (Murrindal Limestone, *perbonus* Zone), plus 36 other specimens from SL46.5m, 58.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO8.5m, 34m (Taravale Formation, *dehiscens* Zone), SLO179m and G.Rd51.2m (Taravale Formation, *perbonus* Zone), Me7.9m, 15.5m, 21.6m, 27.7m, 38.4m, 41.5m (Pyramids Member of Taravale Formation, *dehiscens or perbonus* Zone), Me148.1m, 155.4m, 156.1m (Murrindal Limestone, *perbonus* Zone), and G.Rd340.5m (Taravale Formation, *inversus* Zone).

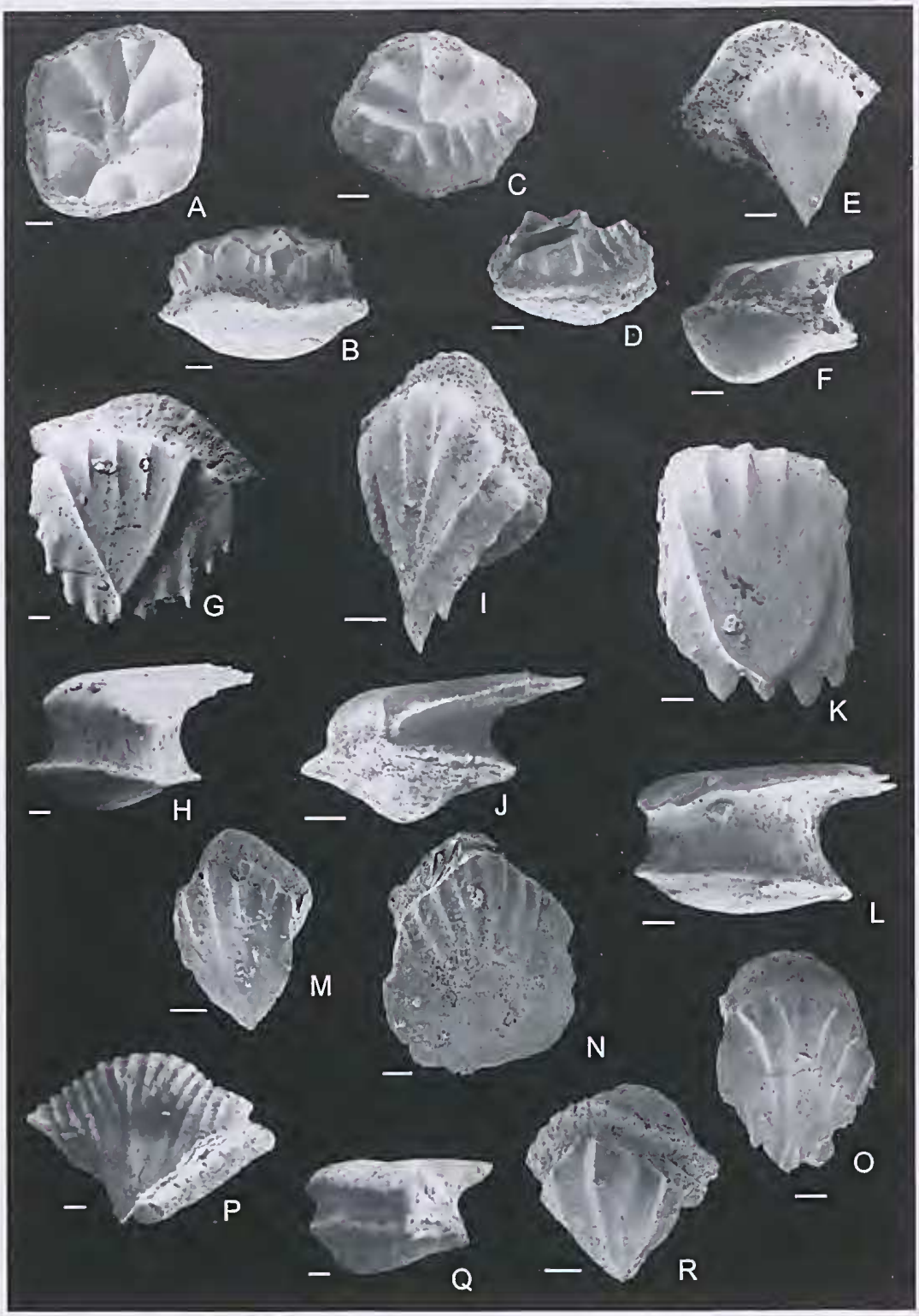
Diagnosis (Wang 1992; emended by Burrow et al. 2000). Crown flat and rhombic, with strongly developed side ridges converging posteriorly and delineating the upper crown which bears ridges on the anterior part. Sharp ridges also lead forward from the posterior point of the crown, ornamenting the dentinous region of the upper neck/lateral crown. The crown is formed of mesodentine comprising rare cell spaces and a network of dentine tubules with a well-developed system of fine, vascular canals; only very rare scales have 'Stranggewebe', and then only in the lower crown. The scale crown is smaller than the base, and the scale neck is low, clearly marked off from the base. Base is convex, with a rhombic outline, bone-cell lacunae, and radiating Sharpey's fibres.

Remarks. This taxon was erected by Wang (1992) for scales from the Ertang Formation of central Guangxi, southern China (*perbonus* Zone), based partly on his interpretation of mesodentine and Stranggewebe in the crown. Burrow (1997) noted the resemblance of similar scales from several central western New South Wales localities (Trundle Group, *kindlei-dehiscens* zones) to scales from Arctic Canada, assigned by Vieth (1980) to *Gomphonchus* sp. Cf. *G. hoppei*. She also noted that Wang's (1992) description included plates showing histological features more typical of *Gomphonchus* than *Nostolepis*: dentine tubules extending into the base, a small embryonic growth zone, numerous thin growth zones in the crown, and absence of Stranggewebe in the crown. On these grounds Burrow (1997) tentatively reassigned the species to "*Gomphonchus*?", and a preliminary report on similar scales from Longmenshan, Sichuan Province, China (*dehiscens-perbonus* zones; Turner *et al.* 1995) followed this designation.

Meanwhile, Valiukevicius (1994) had reassigned Vieth's (1980) *Gomphonchus* sp. cf. *G. hoppei* scales to a new species, *Nostolepis laticristata*, a form lacking the Stranggewebe and wide vascular canals in the crown that are usually present in *Nostolepis*. Further examination of the specimens assigned to *G.? guangxiensis* specimens from NSW revealed one scale has Stranggewebe, and another has wide vascular canals, thus leading Burrow (in Burrow et al. 2000 and Basden et al. 2000) to revert tentatively to the original nomenclature for the taxon, *"Nostolepis" guangxiensis*.

In addition to the scales from China and New South Wales mentioned above, the taxon has been reported from the Point Hibbs Formation, Tasmania (*snlcatus* Zone; Burrow et al. 1998).

Description. Morphology. Scales are small, 0.5-0.7mm, usually of similar width and length. The subrhombic crown is smaller than the base (Fig. 3A, C) and either horizontal or sloping upwards towards the posterior. The main diamond-shaped section of the crown is defined by two ridges converging at a posterior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point, and bears up to three or four anterior ribs that sometimes bifureate at the anterior margin and generally extend almost to the posterior point of the crown. The posterolateral margins of the crown are ornamented by vertical ribs that may also bifureate near the margin with the neck. The neck is generally shallow and of similar depth anteriorly and posteriorly (Fig. 3B). The neck-base margin is distinctly marked by a thin rim. The moderately to deeply convex base is centrally vaulted.

Histology. The base, a low-angled cone, contains bone cell lacunae and radiating Sharpey's fibre bundles. Growth zones are clearly visible in both base and crown. The crown contains Stranggewebe and a network of fine branching dentine tubules.

cf. **Nostolepis** sp.
Fig. 3E, F

Material. AMF101192 from SLO34m (Taravale Formation, *dehiscens* Zone), plus 13 other specimens from G.Rd52.5m (Taravale Formation, *perbonus* Zone), and Me3m, 4.9m, 6.5m, 7.9m, 14m, 27.7m, 33.8m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone).

Remarks. See Denison (1979) for diagnosis and De Pomeroy (1996) for comments on the distribution of this cosmopolitan genus. Nostolepid scales have been recorded from the Early Devonian of eastern Australia in the Broken River Group (*serotinus* Zone) and Martins Well Limestone (*pesavis-sulcatus* zones) in Queensland (Turner 1991, 1993; De Pomeroy 1996; Turner et al. 2000), and the Condobolin Formation, Garra and Windellama limestones, Trundle and Yarra Yarra Creek groups in New South Wales, in horizons dated from Lochkovian to early Emsian (Turner 1991, 1993; Burrow 1997; Basden et al 2000).

Description. Small scales 0.4-0.7mm long and wide. The subtriangular crown slopes up from a rounded anterior margin to a pointed posterior that extends beyond the base (Fig. 3E). Short, low, parallel ridges ornament the anterior part of the crown. The neck is shallow anteriorly and deeper and concave posteriorly (Fig. 3F), with no or few visible pore canal openings. The base and neck are separated by a distinct rim (Fig. 3F). The centrally convex base is subrhombic, with anterior and posterior corners slightly rounded and lateral corners more pointed (Fig. 3E). Faint concentric lines visible on the base possibly represent different growth zones.

Genus **Nostolepoides** Burrow 1997
Nostolepoides platymarginata Burrow 1997
Fig. 3G-L

nostolepid scale – Philip 1965, pl. 8.38. – Turner 1991: pl. 3B.
acanthodian scale – Turner 1991: pl. 5H.
Nostolepoides platymarginata Burrow 1997: 45-57, pl. 1 figs 1-3, pl. 2 figs 7-10,12.
Nostolepoides platymarginata Burrow 1997 – Basden 1999b: 535, pl. 2 figs 2-3.
Nostolepoides platymarginata Burrow 1997 – Burrow 2002: 83-87, figs 5D-I, 8A-K.

Material. AMF101183 from SLO8.5m, AMF112378 from SLO51m (Taravale Formation, *dehiscens* Zone), AMF101185 from SLOc85m (Taravale Formation, *perbonus* Zone), plus 396 specimens from SL39m, 39.7m, 40.8m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL 46m, 48.7m, 58.55m, (Buchan Caves Limestone, *dehiscens* Zone), SLO8.5m, 17m, 34m, 44m, 51m (Taravale Formation, *dehiscens* Zone), SLO55m, 64m, 68m, 72m, 85m, 170m, 179m, 213m and G.Rd 51.2m, 52.5m (Taravale Formation, *perbonus* Zone), Me3.4m, 4.9m, 7.9m, 11m, 15.5m, 18.6m, 21.6m, 24.2m, 27.7m, 30.8m, 36.9m, 41.5m,

Fig. 3. Acanthodian microremains from the Buchan Group. Scale bar = 100μm. A-D, "*Nostolepis*" *guangxiensis*. A, B, Scale AMF101193 from Me41.5-42.7m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. A, crown view, B, lateral view. C, D, Scale AMF101190 from Mc148.1-149.4m, Murrindal Limestone, *perbonus* Zone. C, crown view, D, lateral view. E, F, cf. *Nostolepis* sp. Scale AMF101192 from SLO34m, Taravale Formation, *dehiscens* Zone. E, crown view, F, lateral view. G-L, *Nostolepoides platymarginata* G, H, Scale AMF101183 from SLO8.5m, Taravale Formation, *dehiscens* Zone. G, crown view, H, lateral view. I, J, Scale AMF112378 from SLO51m, Taravale Formation, *dehiscens* Zone. I, crown view, J, lateral view. K, L, Scale AMF101185 from SLO85m, Taravale Formation, *perbonus* Zone. K, crown view, L, lateral view. M, *Cheiracanthoides* sp. cf. *C. comptus*. Scale AMF101215 from Mc88.7m, Murrindal Limestone, *perbonus* Zone, crown view. N, O, *Cheiracanthoides* sp. cf. *C. wangi* N. Scale AMF101214 from SLO213m, Taravale Formation, *perbonus* Zone, crown view. O, Scale AMF101216 from Mc160.6m, Murrindal Limestone, *perbonus* Zone, crown view. P, Q, *Rhadinacanthus*? sp. Scale AMF101189 from SL46.5m, Buchan Caves Limestone, *dehiscens* Zone. P, crown view, Q, lateral view. R, *Gomphonchus bogongensis* Scale AMF101217 from SLO17m, Taravale Formation, *dehiscens* Zone, crown view. Some of these specimens were illustrated by Basden et al. (2000): A, fig. 9.11; C, fig.9.8; E, fig. 9.10; G, fig. 9.1; K, fig. 9.3; P, fig. 9.7.

43m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Mc88.7m, 91.4m, 150.9m, 154m, 155.4m, 156.1m, 156.4m, 160m, 160.6m, 163.8m, 180.1m, 182.9m, 189.9m, 190.5m, 192.5m, 227.4m (Murrindal Limestone, *perbonus* Zone), G.Rd 340.5m (Taravale Formation, *inversus* Zone).

Diagnosis (Burrow 1997). Scales range from 0.15 to 1.0mm wide. They have a bi-level crown; the upper crown is delineated by ridges converging in the posterior half of the crown and with subparallel ribs between them. The lower crown is a latero-posterior, overhanging ledge of varying width and outline. The neck is high and concave (morphotype 1) or low anteriorly (morphotype 2), and the base is moderately vaulted. The crown is composed of mesodentine. Large bone cell lacunae and their processes interconnect throughout the base.

Remarks. These Victorian scales resemble Morphotype 1 scales described by Burrow (1997) from the Gleninga (*pireneae-dehiscens* zones) and Troffs formations (*kindlei-dehiscens* zones) in central NSW. They are morphologically similar to the Late Silurian-Early Devonian *Nostolepis striata* Pander but can be distinguished from that species histologically and by the posterolateral ledge of the crown being wide and/or irregular and continuing around the posterior point, as discussed by Burrow (1997). One of the scales figured by Philip (1965, pl. 8.38) from the Tyers area has been assigned by Burrow (1997) to *Nostolepoides platymarginata*.

Description. Morphology. Scales range in width from 0.5 to 1.2mm. The subrhombic crown consist of two levels. The higher central triangular section is enclosed by two strong radial ridges extending from the anterior margin and converging in a posterior point (Fig. 3G, I), with 3-5 short anterior subparallel ribs that extend up to halfway towards the posterior point, and can bifurcate at the anterior margin (Fig. 3I). The lower level of the crown is a thin posterolateral platform of varying width, that extends beyond the posterior point of the upper crown and can have an irregular (Fig. 3I) or even denticulate margin (Fig. 3G, K). The fairly deep neck is clearly defined, concave, and deeper posteriorly. Some scales have a row of up to ten pore canal openings on the anterior neck (Fig. 3H). The subrhombic base is gently convex, centrally vaulted and separated from the neck by a distinct rim (Fig. 3H, J, L).

Histology. Thin sections show a clear demarcation between crown and base, with a large initial (embryonic) growth zone. Both base and crown have distinct growth zones. The base contains bone cell lacunae and radiating bundles of Sharpey's fibres. The branching dentine tubules in the crown are confined to individual growth zones and are less apparent in outermost zone(s).

Genus **Cheiracanthoides** Wells 1944

Cheiracanthoides sp. cf. **C. comptus**

Fig. 3M

Material. AMF101215 from Mc88.7m (Murrindal Limestone, *perbonus* Zone), and 93 other scales from SL39m, 40.8m (Buchan Caves Limestone, *pireneae* or *dehiscens* Zone), SL46.5m, 58.6m (Buchan Caves Limestone, *dehiscens* Zone), SLO 8.5m, 17m, 34m, 51m (Taravale Formation, *dehiscens* Zone), SLO 55m, 64m, 72m, 85m, 213m and G.Rd50.9m, 52.8m (Taravale Formation, *perbonus* Zone), Mc 15.5m, 33.8m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Mc88.7m, 156.1m, 160.6m, 189.9m, 190.5m (Murrindal Limestone, *perbonus* Zone), G.Rd339.7m (Taravale Formation, *inversus* Zone).

Remarks. The cosmopolitan species *Cheiracanthoides comptus* is frequently reported from Early and Middle Devonian horizons (e.g. Wells 1944; Gross 1973; Denison 1979; Valiukevicius 1979, 1985, 1994, 1998; Vieth 1980; Vieth-Schreiner 1983; Poltnig 1984; Boucot et al. 1989; Turner 1991, 1993; Wang 1992; De Pomeroy 1995, 1996; Basden et al. 2000; Burrow et al. 2000; Zhu 2000; Zhu et al. 2000). Scales from the *Receptaculites* Limestone at Burrinjuck have been assigned to the genus (Giffin 1980, fig. 5), but it is possible that *C. comptus* has become a "bucket" taxon comprising several different form species or even genera with a similar morphology; see De Pomeroy (1996) for discussion.

Recent work has resulted in the erection of several new species (Valiukevicius 1998, Burrow et al. 2000). The diagnosis and description, originally established by Wells (1944), have been refined so that more subtle differences in morphology and histology can be attributed to different species. For example, from material from the East Baltic and Byelorussia, Valiukevicius (1998) has proposed three new species – *Cheiracanthoides plenus* (smaller than *C. comptus*, with fewer ridges on the crown and absence of the

narrow unsculptured rim around the crown anterior), *C. nativus* (lacking the smooth lateral areas on the crown of *C. comptus*) and *C. estonicus* (scales from the Eastern Baltic previously assigned to *C. comptus*). Burrow et al. (2000), studying residues from Sichuan Province, China, have distinguished *C. dolosus*, with a bevelled anterior crown rim, short regularly-spaced ridges, and Stranggewebe extending into the anterior crown, and *C. wangi* (discussed below).

Description. The elliptical or subrhombic crown is flat, slightly wider than long, and ornamented on the anterior third to half by between four and ten radiating or subparallel low rounded ridges separated by broad furrows. The indented neck is a consistent depth from anterior to posterior. The crown extends beyond the base posteriorly. The base is diamond-shaped, moderately convex and and centrally vaulted, with the neck-base margin marked by a thickened rim.

Cheiracanthoides wangi Burrow et al. 2000
Cheiracanthoides sp. cf. **C. wangi**
Fig. 3N, O

Material. AMF101214 from SLO213m (Taravale Formation, *perbonus* Zone), AMF101216 from Me160.6m, and two scales from Me88.7m, 160.6m (Murrindal Limestone, *perbonus* Zone).

Diagnosis. Scales with a fairly flat crown, which is more than twice as long as wide, and with anterior edges often forming a sharp angle. The anterior crown is ornamented with between three and ten sharp, strongly-developed, sub-convergent ridges which extend about one-third of the crown length. The lateral areas of the anterior crown are smooth: i.e., the ridges span the medial two-thirds to three-quarters of the anterior crown. More than half of the crown overhangs the posterior limit of the base; the overhanging section is very thin. The neck is concave all round, falling away sharply from the anterior crown edge, and deepening slightly towards the posterior. The base/neck junction is a strongly marked rim; the base is moderately to strongly vaulted, and projects slightly forwards of the crown. "Stranggewebe" is only formed in the upper neck/crown area of the posterior growth zones. Bone cell lacunae are preserved in the apex of the base (Burrow et al 2000).

Remarks. The species was described by Burrow et al. (2000: 397-398, figs 2.10-2.12, pl. 3.1-3.7, 3.9-3.10) from Longmenshan, Sichuan Province, China (*dehiscens-perbonus* conodont zones), and is also reported from the late Pragian – early Emsian (?*kindlei-perbonus* zones) in the Guangxi and Sichuan provinces (Zhu 2000; Zhu *et* al. 2000). It is now considered an index fossil for the *dehiscens* Zone (Burrow 2000).

The Australian scales described here differ in some features from the Chinese specimens. The central region of the crown generally tends to have ridges closer to parallel, and with a more distinct difference between this central parallel section and the anterior section where the ridges radiate; and the length of the crown, which in some scales is greater than the width, is, even in broken specimens, generally nowhere near twice the width, as is the case with *C. wangi* scales from China. However, since all the Victorian specimens have the thin posterior section of the crown broken off, it is difficult to determine precisely the initial dimensions and length/width ratios of the scales.

Description. Morphology. Scales are approximately 0.8 to 1.2 mm wide, and 0.9 to 1.2 mm from anterior margin to broken posterior edge. The flat subcircular or subrhombic crown slopes slightly upwards towards the posterior. The anterior part of the crown bears between five and seven sharply-crested, radiating ridges that become closer together and subparallel in the central crown area. At the anterior, these ridges can extend down a short distance onto the upper part of the neck. The posterior part of the crown is unornamented, thin and commonly broken.

The neck is generally high and concave, and can become deeper posteriorly. Several small round pore canal openings are found in the central part of the anterior neck, and more elongate openings are high up under the overhanging crown on the posterior neck. The base is very deeply convex, and centrally vaulted. The base and neck are separated by a swollen rim that extends into lateral and posterior flanges.

Histology. The base inserts high into the crown. Both base and crown have distinct growth zones, those in the base parallel to the lower surface. The base contains bone cell lacunae with branching tubules and radiating Sharpey's fibre bundles. All but the outermost growth zones of the crown contain dense outwardly-directed tubules, all confined within individual growth zones.

Family **Diplacanthidae** Woodward 1891
Genus **Rhadinacanthus** Traquair 1888
Rhadinacanthus? sp.

Fig. 3P, Q

Material. AMF101189 from SL46.5m (Buchan Caves Limestone, *dehiscens* Zone) and seven specimens from SL39m (Buchan Caves Limestone, *pireneae* or *dehiseens* Zone), SL46.5m (Buchan Caves Limestone, *dehiscens* Zone), SLO51-68m (Taravale Formation, *perbonus* Zone), and Mc160.6m (Murrindal Limestone, *perbonus* Zone).

Remarks. The genus *Rhadinacanthus* is considered a possible synonym for *Diplacanthus* (Denison 1979; see Burrow et al. 2000, for discussion).

Description. Scales have a kite-shaped crown that is wider than long. The flat crown has a curved anterior margin and pointed lateral and posterior corners (Fig. 3P). The posterior crown overhangs the base only a short distance (Fig. 3Q). Approximately 15 closely-spaced sharp-crested anterior ribs on the crown converge slightly towards the crown centre and extend back to about mid-way.

The indented neck is clearly defined from both crown and base by a distinct rim. The neck has up to ten pore openings low on the neck close to the neck-base margin both anteriorly and posteriorly, but shows no sign of the wart-like bulges at the posterior, as described by Gross (1973) in *R. balticus*. The base is gently convex.

Order **Ischnacanthiformes** Berg 1940
Family **Ischnacanthidae** Woodward 1891
Genus **Gomphonchus** Gross 1971
Gomphonchus? bogongensis Burrow 1997
Fig. 3R

Gomphonchus? bogongensis Burrow 1997: 67-71, pl. 1 figs 9-12, 16, pl. 4 figs 8-16.
Gomphonchus? bogongensis Burrow 1997 – Burrow et al. 1998: 13, fig. 3B-C.
Gomphonchus? bogongensis Burrow 1997 – Basden 1999b: 536-8, pl. 2 figs 8-9.
Ischnacanthid indet. C – Lindley 2002: fig. 9A-I.

Material. AMF101217 from SLO17m (Taravale Formation, *dehiscens* Zone), and 152 specimens from SLO39m, 40.8m (Buchan Caves Limestone, *pireneae* or *dehiseens* Zone), SL46.5m, 48.7m, 53.2m, 54m, 56.2m, 58.5m (Buchan Caves Limestone, *dehiseens* Zone), SLO8.5m (Taravale Formation, *dehiscens* Zone), SLO170m, 213m, G.Rd51.7m, 52.5m (Taravale Formation, *perbonus* Zone), Mc 4.9m, 6.5m, 8.5m, 11m, 14m, 15.5m, 18.6m, 30.8m, 33.8m, 35.4m, 36.9m, 38.4m, 43m, 44.5m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Mc150.9m, 154m, 155.4m, 156.1m (Murrindal Limestone, *perbonus* Zone).

Diagnosis (Burrow 1997). Small scales, 0.15 to 0.7mm wide, with a subtriangular crown, low neck, and a moderate to large convex base. There are two main morphotypes: in morphotype 1, the crown has a curved fan shape, ornamented with sharp fan-like ridges and grooves, and slopes upwards from the anterior edge to a posterior point. Morphotype 2 scales have a crown with an upper sub-triangular, and a lower lateral, level which can be greatly elongated posteriorly. The scale crown is composed of orthodentine. All scales have a 'scalloped' antero-lateral crown edge.

Remarks. Scales resemble Morphotypes 1 and 2 described by Burrow (1997) from the Trundle Beds (now Troffs Formation) and Gleninga Formation in central NSW. Revised dating of the horizons by Sherwin (1996) now places the horizons with these scales into *pireneae-dehiscens* zones. Scales of *G.? bogongensis* are also reported from the *sulcatus* Zone at Point Hibbs (Burrow et al. 1998).

Morphotypes 1 and 2 can both be distinguished from *Nostolepoides platymaginata* scales by the scalloped anterior margin of the crown, and the increased depth of the neck towards the posterior, and Morphotype 1 also by the lack of lowered lateral crown ledges. Morphotype 1 is distinguished from *"Nostolepis" guangxiensis* by the short anterolateral ridges not continuing around below the posterior point of the crown (Burrow 1997).

Description. Morphology. Subrhombic or diamond-shaped scales have the crown and base approximately a similar shape, and the crown generally smaller than the base. Width ranges from 0.4 to 1.2mm. The fan-shaped crown has 4-8 radiating anterior ridges with sharp crests, separated by deep furrows; these ridges can be less than half the crown length, or extend virtually to the posterior point of the crown. These features in combination with the curving down of the anterior crown towards the neck give the scalloped anterior margin to the crown that is distinctive of this form.

In Morphotype 2 scales the posterior point of the crown is more elongated than in Morphotype 1, and can extend slightly beyond the base. Short anterolateral

ridges on the sides of the crown do not continue beyond the posterior point. These anterolateral ridges vary, from very short anterior ridges that give a bifurcating appearance to the marginal lateral ribs of the crown, or do not even quite meet the marginal lateral ribs, to ridges found high on the lateral margins of the crown, not extending far onto the neck.

The neck is short anteriorly, not very indented, and widens posteriorly. A row of pore canal openings on the posterior neck is better developed in some scales, with the canal openings elongated.

The base is moderately to strongly convex, centrally vaulted and separated from the neck by a distinct rim that is particularly pronounced at the lateral and posterior corners. Concentric markings parallel to the neck/base rim indicate presence of Sharpey's fibres.

Histology. Scales are generally not well preserved, with minimal histological detail revealed in many scales. However, growth zones in both base and crown are apparent. The base contains Sharpey's fibre bundles, a fine network of interconnecting tubules, and sparse bone cell lacunae. The crown contains fine branching tubules that are sparse in the outermost growth zone.

Class **Osteichthyes** Huxley 1880
Subclass **Actinopterygii** Klein 1885
Order **Palaeonisciformes** Hay 1929
Ligulalepis Schultze 1968
Ligulalepis toombsi Schultze 1968
Fig. 4A

Ligulalepis toombsi Schultze 1968: 345-351, figs 1-6, pl. 1 figs 1-8, pl. 4, fig. 1.
Ligulalepis toombsi Schultze 1968 – Giffin 1980: 10-11, fig. 10.
Ligulalepis toombsi Schultze 1968 – Burrow 1994: 177-184, figs 2-5.
Ligulalepis toombsi Schultze 1968 – Basden et al. 2000: fig. 8.7.

Material. AMF 101178 from SLO34m (Taravale Formation, *dehiscens* Zone).

Diagnosis (translated from Schultze 1968). Genus ... with deep scales on the flanks; scales close to the shoulder girdle are 3-4 times deeper than long; on the anterior upper corner there is a very marked projection, which makes a sharp angle to the front edge; ventral edge slopes away from the front edge towards the back end. Strong peg and correspondingly deep socket; keel quite deep; secondary keel, on the back edge of which are openings of most canals. Development of the ganoin surface common to all species in the genus. Ganoin well-developed, partly divided into separate ribs backwards from front edge, ornamented towards front edge with small longitudinal striations which are absent in small scales; back edge comb-like; front edge slightly or strongly concave, anterior lower corner rounded, ventral edge straight.

Remarks. Schultze (1968) erected the taxon from material in residues from the 1955 and 1963 Burrinjuck expeditions by H.A. Toombs (Natural History Museum, London), from spot localities in horizons from the Cavan Formation to the Warroo Limestone. Giffin (1980) figured similar scales from the *Receptaculites* Limestone at Taemas (residues of B.D.E. Chatterton's processing of trilobites and brachiopods) as did Burrow (1994) from the Trolls and Gleninga formations of central New South Wales (*pireneae-dehiscens* zones). Other Devonian palaeoniscoid genera described from Australia are *Terenolepis turnerae* Burrow 1995 from Connemarra Formation, Trundle Group and Garra Limestone (Hocking in Basden et al 2000), *Howqualepis rostridens* from the Frasnian Avon River Group at Mt Howitt, Victoria (Long 1988, figs 32, 33), and *Minia toombsi* and *Moythomasia durgaringa* from the Givetian-Frasnian Gneudna Formation and Frasnian Gogo Formation (Gardiner & Bartram 1977; Trinajstic 1999a, figs 3, 4; 1999b, figs 4, 5).

Description. The subrectangular scale has a free field ornamented with unfused ridges, a denticulate caudal margin and a smooth depressed field along the curved rostral edge. A rounded, tongue-shaped process projects rostro-dorsally and more pointed dorsal peg would have fitted into a corresponding socket on the ventral edge of the scale above. On the basal surface dorsoventrally oriented primary and secondary keels are separated by a groove.

Subclass **Sarcopterygii** Romer 1955
Division **Rhipidistia** Cope 1887
Order **Onychodontiformes**
Onychodontiformes gen. et sp. indet.
Fig. 4B-J

Material. Scales with U-shaped tubercles: AMF118232 from Mc7.9-9.1m (Pyramids Member

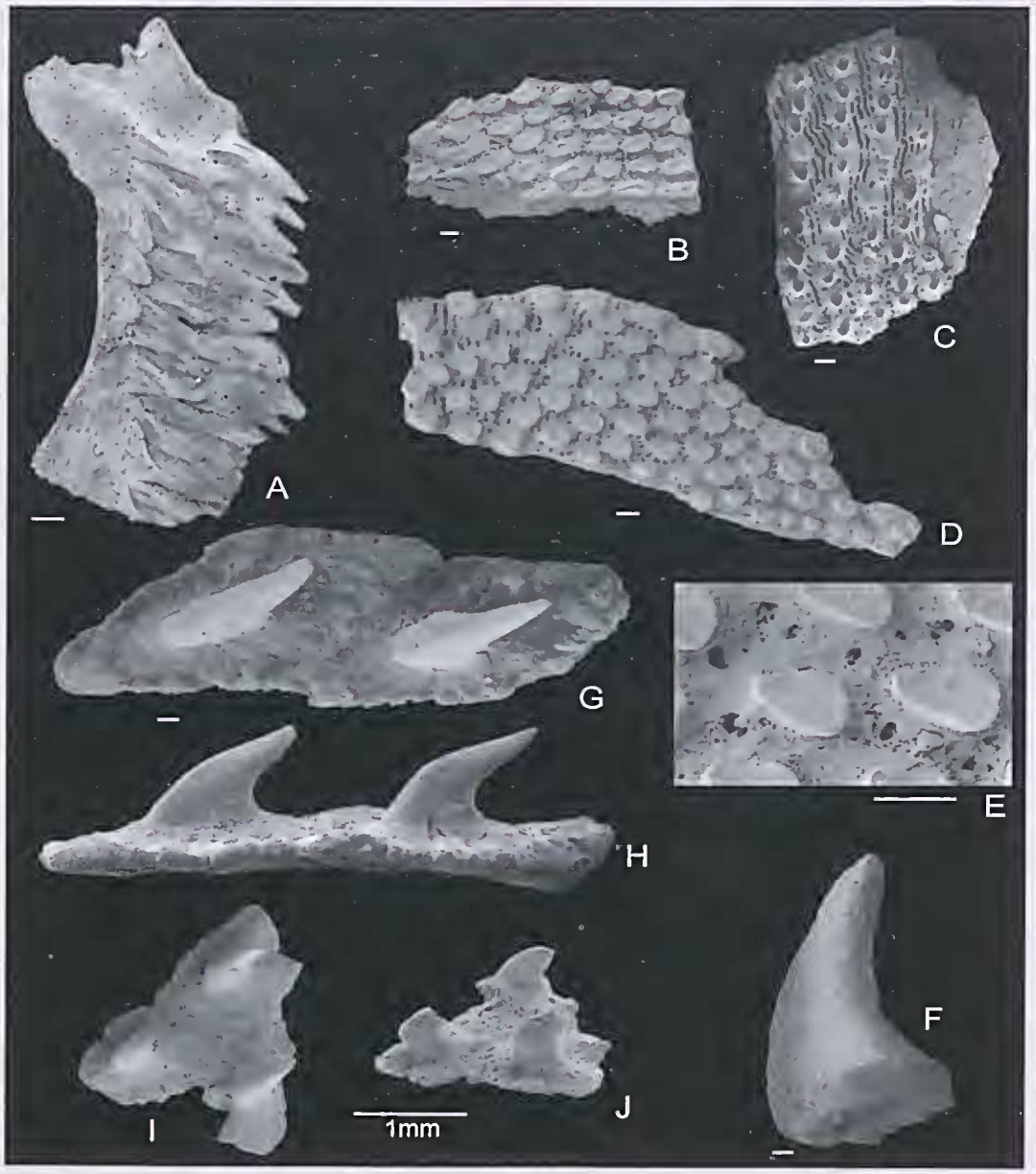

Fig. 4. Osteichthyan microremains from the Buchan Group. Scale bar = 100μm unless indicated otherwise. A, *Ligulalepis toombsi* Scale AMF101178 from SLO34m, Taravale Formation, *dehiscens* Zone. B-J, Onychodontiformes gen. et sp. indet. B, Fragment AMF118232 from Mc7.9-9.1m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone, crown view. C, Fragment AMF101181 from Mc156.1m, Murrindal Limestone, *perbonus* Zone, crown view. D, E, Fragment AMF118231 from GRd340.5m, Taravale Formation, *perbonus* Zone. D, crown view, E, detail of crown ornament. F, Tooth AMF101220 from SLO55m, Taravale Formation, *perbonus* Zone. G, I1, Scale AMF101182 from Mc43-44.2m, Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone. G, crown view, I1, lateral view. I, J, Scale AMF118236 from GRd340.5m, Taravale Formation, *inversus* Zone. I, crown view, J, coronolateral view. Some of these specimens were illustrated by Basden et al. (2000): A, fig. 8.7; C, fig. 8.10; G, fig. 8.11; I1, fig. 8.12.

of Taravale Formation, *dehiscens* or *perbonus* Zone), AMF101181 from Me156.1m (Murrindal Limestone, *perbonus* Zone), AMF118231 from G.Rd340.5m (Taravale Formation, *perbonus* Zone), plus 37 other specimens from G.Rd340.5m (Taravale Formation, *perbonus* Zone), Mc3m, 7.9-9.1m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Me151.5m (Murrindal Limestone, *perbonus* Zone).
Teeth: AMF101229 from SLO55m (Taravale formation, *perbonus* Zone), plus 157 other specimens from SLO8.5m, 17m, 34m, 44m, 51m (Taravale Formation, *dehiscens* Zone), SLO64m, 213m, G.Rd50.9m, 52.3m (Taravale Formation, *perbonus* Zone), Me3m, 3.4-3.6m, 4.9-6.2m, 6.5-7.6m, 7.9-9.1m, 11-12.2m, 12.5-13.7m, 14-15.2m, 15.5-18.3m, 17.7m, 18.6-21.3m, 21.6-24.4m, 24.4-27.4m, 27.7-30.5m, 30.8-33.5m, 33.8-35.1m, 35.4-36.6m, 36.9-38.1m, 38.4-39.9m, 43-44.2m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), Me91.4-93m, 150.9m, 151.5m, 155.4m, 156.1m, 156.4m, 160.6m, 161.5m, 163.1m, 163.8m, 192.5m (Murrindal Limestone, *perbonus* Zone), Me224-225.6m, 225.9-227.1m, 227.4-228.6m (Upper Taravale Formation, *perbonus* Zone), G.Rd340.5m (Taravale Formation, *inversus* Zone).

Scales with curved denticle: AMF101182 from Mc43-44.2m (Pyramids Member of Taravale Formation, *dehiscens* or *perbonus* Zone), AMF118236 from G.Rd340.5m (Taravale Formation, *inversus* Zone).

Remarks. Inclined U-shaped tubercles with a central depression are found on scales of several fish groups, thus limiting their utility for identification. Dipnoan scales have been described with this type of tubercular ornament in conjunction with cosmine and Westoll lines (the primitive dipnoan *Dipnorhynchus sussmilchi* from Buchan and Taemas; Thomson & Campbell 1971), but as no cosmine is preserved on the Victorian scales, dipnoan affinity is probably precluded. Apart from dipnoans, the only other common osteichthyan remains known from the region are actinopterygians and onychodontids, and since actinopterygians are not known to have denticles, the scales and fragments described here probably belong to onychodonts.

Description. Scales with U-shaped tubercles. Figured specimens are broken fragments that exhibit a variety of morphologies of the crescent- or U-shaped tubercles. The tubercles themselves can be fairly flat with smooth, very slightly concave anterior margins (Fig. 4D), oriented in rows (Fig. 4C), or more elongate and irregularly shaped with a distinct depression in the anterior face (Fig. 4B).

The detail of specimen AMF118231 (Fig. 4E) shows the bone surface between the dentine tubercles pitted with irregular vascular canal openings, whereas in AMF101181 (Fig. 4C) the bone between the tubercles is striated by rows of elongate canal openings.

Teeth. Simple curved conical teeth up to 2mm long can be slender, tapering to a sharp point, or thicker with a rounded apex (Fig. 4F). The base of the laniary and interlaniary teeth is circular and constricted. All specimens are hollow, with the cusp in better-preserved examples covered in finely striated enamel, although preservation is not sufficient to discern micro-patterns in the enamel.

Scales with curved denticle. Articulated diamond-shaped scales (Fig. 4G) have a central curved, inclined, conical, unstriated denticle. The main part of the scale consists of flat bony tissue; in contrast, the denticles are noticeably smoother and shinier. The only ornament on the scales is a series of faint radiating grooves on the base around each denticle (Fig. 4I, J). The basal surface of the scales generally is flat and unornamented, although specimen AMF101182 (Fig. 4G, H) has faint grooves corresponding to the margins of the articulated diamond-shaped scales, and the three articulated scales in specimen AMF118236 (Fig. 4I, J) are slightly concave centrally. A broken denticle (Fig. 4I, J) shows a very narrow longitudinal canal, situated slightly off-centre towards the outer edge of the denticle.

CONCLUDING REMARKS

Acanthodian scales are the most common elements of the fauna (Fig. 3). Climatiid scales of *Nostolepoides platymarginata* and *Cheiracanthoides* sp. cf. *C. comptus* are spread throughout the three sections, and occur in all four formations (Buchan Caves and Murrindal limestones, Taravale Formation, and the Pyramids Member of the Taravale Formation). In SL/SLO section, *Gomphonchus? bogongensis* is much more common in the Buchan Caves Limestone.

The "nostolepid" scale (*sulcatus* Zone) from Tyers in Victoria, illustrated by Philip (1965) and Turner (1991, pl. 3B), is similar to some of these scales, but another similar scale was assigned by Vieth (1980, pl. 6, fig. 15) to *Cheiracanthoides comptus*. More elongate scales (e.g. Fig. 3E, F) resemble the scale from

Burrinjuck in southern New South Wales assigned to *C. comptus* by Giffin (1980, fig. 5), but these are also similar to a scale from Algeria assigned by Blieck et al. (1984, pl. 1, fig. 4) to *Nostolepis* sp. Similar crown morphologies but different shape (Fig. 3G-L) might indicate scales from different parts of the same fish, but V.T.Young (1995) recorded little shape variation in several articulated acanthodian taxa from the Early to Middle Devonian of Britain. Other scales are compared with *Cheiracanthoides wangi* (Fig. 3N, O), recently described from *dehiscens-perbonus* zones of China (Burrow et al. 2000), and *Rhadinacanthus* (Fig. 3P, Q).

Scales of arthrodires *Goodradigbeeon* and *Buchanosteus* are the most abundant placoderm microremains in the Buchan measured stratigraphic sections. Small plate fragments (Fig. 2E, F) recorded from horizons in the *dehiscens – inversus* interval have the same ornament as originally figured by White (1952, pl. 30) for *Buchanosteus murrumbidgeensis*. Other plate fragments with more elongate tubercles (Fig. 2A) are compared with *Murrindalaspis* sp. (e.g. Long & Young 1988).

Osteichthyan remains from Buchan include a scale of the actinopterygian *Ligulalepis toombsi* (Fig. 4A), and cosmine covered elements that may belong to either dipnoans or porolepiforms (see De Pomeroy, 1996: 433). Similar cosmine-covered scales described from an Early Devonian dipnoan by Barwick et al. (1997) have rows of odontodes as seen in porolepiform scales, (e.g. Fig. 4B-E; Ørvig, 1969, fig. 6). However, the scales of *Dipnorhynchus*, the only named dipnoan from Buchan, have a different morphology, with coarser rounded tubercles on the scale margins (see Thomson & Campbell 1971, figs 86-89). By the Late Devonian these tubercle zones had been lost from dipnoan scales (Pridmore & Barwick 1993). Rhombic plates, each with a central hooked denticle (Fig. 4G-J) may be small elements from inside the buccopharyngeal cavity of an onychodontid (P.Janvier, pers. comm.). In section SL/SLO, both osteichthyans present (*Ligulalepis toombsi* and *Onychodus* sp.) occurred only in the Taravale Formation, and were absent from the Buchan Caves Limestone.

A chondrichthyan scale similar to *Ohiolepis* sp. (Fig. 2K) is the first chondrichthyan reported from the Buchan sequence.

The first thelodont scales described from the Buchan area were part of the current study (Basden 1999a). All ten scales were recovered from horizons dated *dehiscens-perbonus* zones, and have been assigned to *Turinia* sp.cf. *T. australiensis*.

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